Comparing model parameterizations of the biophysical impacts of ocean acidification to identify limitations and uncertainties

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ABSTRACT

Ocean acidification (OA) driven by anthropogenic CO_2 emissions affects marine ecosystems, fisheries and aquaculture. Assessing the impacts of OA using projection models facilitates the development of future scenarios and potential solutions. Here, we explored various ways to incorporate OA impacts into a multi-stressor dynamic bioclimatic envelope model to project biogeographic changes of ten commercially exploited invertebrate species. We examine three dimensions of uncertainties in modelling biophysical OA effects: model structure, parameterization, and scenario uncertainty. Our results show that projected OA impacts are most sensitive to the choice of structural relationship between OA and biological responses, followed by the choice of climate change emission scenarios and parameterizations of the size of OA effects. Species generally showed negative effects to OA but sensitivity to the various sources of uncertainty were not consistent across or within species. For example, some species showed higher sensitivity to structural uncertainty and very low sensitivity to parameter uncertainty, while others showed greatest sensitivity to parameter uncertainty. This variability is largely due to geographic variability and difference in life history traits used to parameterize model simulations. Our model highlights the variability across the sources of uncertainty and contributes to the development of integrating OA impacts in species distribution models. We further stress the importance of defining the limitations and assumptions, as well as exploring the range of uncertainties associated with modelling OA impacts.

1. Introduction

Carbon dioxide (CO_2) emissions from human activities such as the burning of fossil fuels largely contributes to the rapid rate of ocean acidification (OA) since the industrial revolution (IPCC, 2013). OA is the chemical process driven by elevated atmospheric CO_2 that results in reduced pH and increased acidity. Global sea surface pH has already decreased by 0.1 units since the pre-industrial average of 8.17, a 26% increase in acidity (Caldeira and Wickett, 2003; Feely et al., 2009; Pörtner et al., 2014). Under our current emissions trajectory, sea surface pH is projected to decrease by an additional 0.3 units by the end of the 21st century (Ciais et al., 2013; IPCC, 2013). Some areas are experiencing much larger changes in pH. For example, the Northeast Pacific Ocean has naturally fluctuating pH levels due to upwelling, and the uptake of anthropogenic CO_2 is elevating acidification across these areas (Feely et al., 2014; Haigh et al., 2015).

Ocean acidification is expected to impact marine organisms, communities and ecosystems (Branch et al., 2013; Cooley et al., 2009; Doney et al., 2012; Guinotte and Fabry, 2008; Haigh et al., 2015; Le Quesne and Pinnegar, 2012; Mathis et al., 2015), with variations in sensitivity across populations, taxonomic groups and ecosystem types (Heuer and Grosell, 2014; Kroeker et al., 2013; Nagelkerken and Connell, 2015). Most notably, OA compromises the ability of organisms to efficiently build and retain calcium carbonate structures (e.g. coral reefs, oyster and mussel shells, coccolithophore exoskeletons) due to the under-saturation of calcium carbonate (Fabry et al., 2008; Feely et al., 2004; Kleypas et al., 2006; Nienhuis et al., 2010; Ries et al., 2009). Beyond calcification, OA affects a wide range of physiological processes such as acid-base balance, basal metabolic rates, aerobic scope, oxygen consumption, thermal tolerance, fertilization rates, and development, among others (detailed in Le Quesne and Pinnegar, 2012). Direct impacts of OA on changes in species abundance will result in important changes to competitive, facilitative, and trophic relationships (Dutkiewicz et al., 2015; Queirós et al., 2015; Sunday et al., 2017; Trenkel et al., 2005). Overall, changes in physiology and behaviour lead to changes in growth and abundance, and when considered across multiple interacting species, results in important changes in community structure and ecosystem function (Kroeker et al., 2013; Nagelkerken

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and Connell, 2015).

OA coincides with other anthropogenic CO_2 driven stressors including ocean warming and decreases in dissolved oxygen concentration. Increases in temperature affects physiological processes such as metabolism, increasing the demand for oxygen and reducing aerobic scope (Pörtner and Lannig, 2009). Decreases in oxygen content further exacerbates this effect, and is projected to lower the metabolic capacity of marine habitats potentially leading to decreased body size (Cheung et al., 2013a; Deutsch et al., 2015; Pauly and Cheung, 2017). Biogeographic responses to ocean warming and decreased oxygen content have been observed as shifts in distributions to deeper and higher latitudinal waters (Cheung et al., 2013b; Dulvy et al., 2008; Perry et al., 2005). While isolating the effects of OA is important for understanding the mechanisms in which OA effects operate, integrating OA with other stressors provides a more real-world application of the effects of anthropogenic-influenced global changes on species distribution and abundance.

The inclusion of OA in assessing impacts of anthropogenic CO_2 emissions is important in developing scenarios of future global change for marine systems. Published syntheses and meta-analyses are extremely useful for providing baseline parameters for modelling and assessing the biological impacts of OA (Kroeker et al., 2013; Nagelkerken and Connell, 2015; Sunday et al., 2017). They also provide a basis for linking complex physiological responses to life history traits that have direct implications on population dynamics. For example, Cheung et al. (2011) incorporated physiological models into a dynamic bioclimatic envelope model (Cheung et al., 2008) to assess climate change effects on species distribution and abundance. This model was then applied to a socioeconomic analysis of climate change and OA impacts in the Arctic Ocean (Lam et al., 2014). Empirical models of OA effects have also been used to estimate changes in the growth rates of mollusc species and thereby impacts on US mollusc fisheries (Moore, 2015; Ries et al., 2009). Another promising approach incorporates information about marine food webs by using an ecosystem model to model the impacts of OA on functional groups that include harvested taxa (Ainsworth et al., 2011).

Projection models provide valuable insight to potential future scenarios but are subject to various sources of uncertainty. Uncertainty when modelling ocean acidification arises from the choice of model parameterizations, which produce a range of possible impact pathways. We define three sources of uncertainty when modelling OA impacts: 1) structural, 2) parameter, and 3) scenario uncertainty (Hawkins and Sutton, 2009). Structural uncertainty refers to the underlying construction of the model, such as the mathematical formulation of a model to represent ecological relationships, or the processes modelled using correlative versus mechanistic approaches (e.g. Pauly et al., 2000). Parameter uncertainty stems from the inherent variability and our limited ability to accurately and precisely measure biological processes and relationships (e.g. Kremer, 1983). Scenario uncertainty results from the different possible future pathways due to many socioeconomic factors (e.g. governmental policies, technological development) that affect biophysical drivers. This includes the various greenhouse gas concentration trajectories used to drive climate and biophysical models (IPCC, 2013). The combined uncertainties produce the full range of future trajectories, providing valuable insight to the sensitivities of modelling OA impacts.

In this study, we explored various ways to incorporate OA impacts into a multi-stressor dynamic bioclimatic envelope model to project changes in the biogeography of ten commercially exploited invertebrate species. We examined the structural, parameterization and scenario uncertainties in modelling OA effects. To eventually improve our confidence in forecasting future scenarios, we explored the variability of model outputs and discussed the utilities and limitations of different ways to incorporate OA impacts in spatial biogeographic models.

2. Methods

We incorporated the impacts of OA into a previously developed dynamic bioclimatic envelope model (DBEM) (Cheung et al., 2016a, 2011, 2008) to estimate changes in species distribution and abundance. The DBEM uses earth system models as inputs (e.g. Dunne et al., 2013) and links species distribution models (Jones et al., 2012), advection-diffusion movement models (Sibert et al., 1999), growth models (Pauly, 1980), physiological models (Pauly, 1981), and population dynamics models (Hilborn and Walters, 1992; O'Connor et al., 2007; Pauly, 1980) to predict how species will move geographically across time (annual time step) and space (on a 0.5° latitude x 0.5° longitude grid) with climate change. We outline the specifics of modelling the effects of OA and how it interacts with effects from other stressors (i.e. temperature and oxygen) below, while other details on the DBEM can be found in the Supplementary material (Supplementary Fig. S1).

2.1. Modelling the effects of global change

Global change effects on organisms and populations include changes in temperature, oxygen and pH. We integrated the biological impacts of OA on exploited populations through the effects on somatic growth and mortality rates. We define the effects on somatic growth as a mechanistic process, and the effects on survival as a correlative process. First, the model uses the von Bertalanffy growth function (von Bertalanffy, 1951) to simulate changes in growth in response to ocean warming, decreases in dissolved oxygen concentration, and ocean acidification (Cheung et al., 2011). Growth rate (change in biomass, B, as a function of time, t) is determined with the derived equation from a growth function:

$$\frac{dB}{dt} = HW^d - kW^b \tag{1}$$

where H and k represent the coefficients for anabolism and catabolism, respectively. Anabolism scales with body weight (W) to the exponent $d < 1$, catabolism scales linearly with (W), i.e. $b = 1$, and their difference determines the growth rate of species biomass (B). Solving for $dB/dt = 0$ when asymptotic weight (W_∞) is reached, we obtained $H = kW_\infty^{(1-d)}$. Thus, growth rate is dependent on the available oxygen (anabolism) and oxygen demand for maintenance metabolism (catabolism).

Integrating Eq. (1) into a generalized von Bertalanffy growth function:

$$W_t = W_\infty \left[1 - e^{-K(t-t_0)} \right]^{1/(1-d)} \tag{2}$$

where K is the von Bertalanffy growth parameter where $K = k(1-d)$. The von Bertalanffy growth parameter K represents the rate at which maximum body size is reached. We assume $d = 0.7$, although values typically range from 0.5 and 0.95 across invertebrate species (Hughes, 1983; Johnson and Rees, 1988; Jones et al., 1992). Sensitivity of maximum body size to changes in temperature and acidity show that low values of d (< 0.7) results in slight decreases in sensitivity, while larger values of d (> 0.7) results in major increases in sensitivity (Supplementary Table S1) (Pauly and Cheung, 2017). Effects of multiple stressors show an antagonistic interaction for the effects on body size. Therefore, the use of 0.7 for all species considered here are conservative as smaller values of d do not considerably change temperature and acidity effects on maximum body size, while larger values of d only increase sensitivity.

The effects of temperature were modelled to affect metabolism—described in Eqs. (3) and (4)—through the H and k coefficients following the Arrhenius equation, $e^{-j/T}$, where $j = E_a/R$, with E_a and R equal to the activation energy and Boltzmann constant, respectively. Furthermore, oxygen availability affects aerobic scope (i.e. oxygen supply) while acidification affects maintenance metabolism (i.e. oxygen demand). We modelled the impacts of decreases in oxygen and ocean
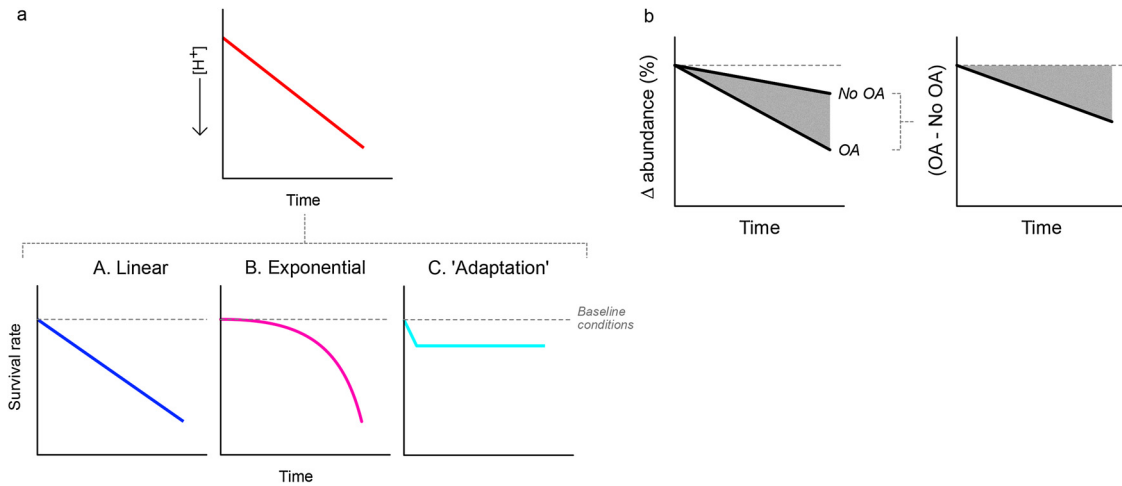
Fig. 1. a) Conceptual diagram illustrating the scenarios of various relationships between $[H^+]$ and survival rate explored in this study, under a hypothetical linear change in acidity over time. Survival rate is used here as an example that can be applied to other biological parameters impacted by ocean acidification (OA). b) Diagram of how we presented our results by isolating the net impacts of OA on abundance by taking the differences between model outputs with OA and no OA effects.

acidification following the most viable current working oxygen- and capacity- limited thermal tolerance hypothesis, which assumes that deviations from optimal environmental conditions (e.g. temperature, acidity) decreases aerobic scope and thus the energy available for growth. (Pörtner, 2008; Pörtner and Farrell, 2008). These effects can be modelled in the form:

$$H = g[O_2]e^{-j_1/T} \tag{3}$$

and

$$k = h[H^+]e^{-j_2/T} \tag{4}$$

The constants j_1 and j_2 are equal to E_a/R where E_a (for anabolism and catabolism, respectively) and R are the activation energy and Boltzmann constant, respectively, while T is the absolute temperature (in Kelvin) (Cheung et al., 2011). Changes in the concentration of oxygen $[O_2]$ and hydrogen ions $[H^+]$ relative to initial conditions thus change H and k, respectively. The coefficients g and h from Eqs. (3) and (4), respectively, were derived for each species from the average W_∞, K, and environmental temperature T_0 reported in the literature (Cheung et al., 2011):

$$g = \frac{W_\infty^{(1-d)}K}{[O_2]e^{-j_1/T}} \tag{5}$$

and

$$h = \frac{K/(1-d)}{[H^+]e^{-j_2/T}} \tag{6}$$

The model predicts changes in life history parameters due to changes in temperature, oxygen availability, and pH for asymptotic weight (W_∞) and von Bertalanffy growth parameter K:

$$W_\infty = \left(\frac{H}{k}\right)^{1/(1-d)} \tag{7}$$

and

$$K = k(1-d) \tag{8}$$

Other parameters that scale with weight can also be predicted, including asymptotic length and the length at maturity (Beverton and Holt, 1959).

Natural population mortality rates (M) were estimated from the empirical equation (Pauly, 1980):

$$M = -0.4851 - 0.0824\log(W_\infty) + 0.6757\log(K) + 0.4687\log(T') \tag{9}$$

where T' is the average water temperature of a species range in degrees Celsius—other parameters are defined above. Pauly's (1980) model was used here because of data availability and its widespread used for fish stocks and in fisheries assessments; we address the scope of using alternative empirical equations in the discussion section. Thus, our model incorporates trade-offs between basal metabolism and aerobic scope, ultimately affecting life history traits of growth, maximum body size, and mortality rate. Additionally, at the population level, changes in growth parameters affect mean body size and fecundity.

The construction of our model uses a mixed approach and incorporates both mechanistic and correlative models. OA effects on growth (mechanistic model) operate at multiple levels throughout the DBEM, and have downstream effects on maximum weight (Eq. (7)), growth rate (Eq. (8)), and mortality rate (Eq. (9)). OA effects on survival (correlative model) were modelled to directly affect population mortality for both larval and adult stages, such that changes in $[H^+]$ results in changes in the population mortality rate (M) (Eq. (9)).

Growth and survival rates change accordingly with changes in pH, which we measure here as hydrogen ion concentration, $[H^+]$. We used parameters from a meta-analysis for the effects of OA on life history traits (Kroeker et al., 2013). We modelled the effects of OA under the assumption that the parameter values represent a percent change in growth or survivorship with a doubling of $[H^+]$.

2.2. Characterizing uncertainties

We explored three possible sources of uncertainty in modelling the effects of OA: structural, parameter, and scenario uncertainty. First, we focus on structural uncertainty as the inaccuracy in the modelled relationship between $[H^+]$ and life history rates (i.e. somatic growth rate and survival rate). To establish relationships between $[H^+]$ and life history traits, we used parameter values from Kroeker et al. (2013), which are point estimates for a given minimum change in pH. Unfortunately, no information on the relationship between these point estimates was available and previous studies have shown variation across species (Ries et al., 2009). We considered three possible ways to represent the structural relationship between $[H^+]$ and life history rates and tested the sensitivity of the model projections to each underlying relationship. Fig. 1 illustrates the various options for which we make assumptions about the relationship. For option A we scaled changes in $[H^+]$ linearly with life history rates relative to initial conditions, reflecting a scenario in which a species' sensitivity to OA is similar at low and high levels of acidity. This represents our baseline model, i.e.

Table 1

Effect sizes (with 95% confidence limits in parentheses) of OA impacts on life history traits (modified from Kroeker et al., 2013).

	Growth[a] Mean (Lower, Upper)	Survival[a] Mean (Lower, Upper)
Crustaceans	−16% (−33, 6)	−13% (−25, 0)
Molluscs	−17% (−26, −10)	−35% (−56, −10)

[a] Effect sizes represent the percent change with a doubling of hydrogen ion concentration.

$$Surv_t = Surv_{init} * \left[1 + \left(Per * \left(\frac{[H^+]_t}{[H^+]_{init}} - 1 \right)^w \right) \right]$$

(10)

Surv is the survival rate per year and used here as an example but can be applied to other biological characteristics affected by OA (e.g. growth, reproduction, calcification). Survival rate in year t is derived from the initial (*init*) survival rate and the relative change in $[H^+]$ between year t and initial $[H^+]$ conditions. *Per* represents the value used from Kroeker et al. (2013) for the percent change in survival rate with a doubling of $[H^+]$ (Table 1). The exponent w is equal to 1 in the linear model. For option B we used an exponential model, which reflects a scenario in which a species' sensitivity to OA increases with increasing $[H^+]$. Using Eq. (10), the exponent w is set to 2. Changes in $[H^+]$ in these two scenarios are expressed relative to initial conditions, defined as the average $[H^+]$ between years 1971 and 2000. For option C we explored an 'adaptation' scenario, where species are assumed to acclimatize or adapt to recent changes in pH. This scenario is represented by expressing changes in pH relative to a moving window of the previous year, i.e. where in Eq. (10) $[H^+]_{init}$ is substituted with $[H^+]_{t-1}$ and survival rate in year t is calculated from the relative change in $[H^+]$ between year t and the previous year $t - 1$. The adaptation scenario assumes a linear relationship between $[H^+]$ and the biological traits affected by OA, and further assumes that acclimatization and/or adaptation has a fixed time lag but that the capacity for adaptation is limitless.

We compare differences between the results from mechanistic and correlative models for OA effects (described above) as an additional source of structural uncertainty. Furthermore, we included simulations using different earth system models, which have different structural characteristics such as grid resolution and marine biogeochemical components (Bopp et al., 2013). We used three earth system models: NOAA's Geophysical Fluid Dynamics Laboratory (GFDL-ESM); Max Planck Institute for Meteorology (MPI-ESM); and Institute Pierre Simon Laplace Climate Modelling Centre (IPSL-ESM). These models were chosen as they provide high-resolution (1° longitude x 1° latitude) sea surface and bottom data, as well as all the environmental data required by the DBEM (Cheung et al., 2016b).

To characterize parameter uncertainty, we generalized OA effects based on taxonomic group and simulated the impacts of OA with the high and low 95% confidence limit values provided in Kroeker et al. (2013) (Table 1). While species-specific parameters do exist (Ries et al., 2009), we chose to use generalized values to make comparisons of the sensitivity of our results to this source of uncertainty.

Lastly, we characterized scenario uncertainty by using the different representative concentration pathways (RCP), which uses atmospheric greenhouse gas concentration scenarios to drive other environmental variables. There are four RCP scenarios commonly used: RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5. The numbers represent radiative forcing values in the year 2100 relative to pre-industrial periods under specific emissions scenarios. We labelled our pathways as Low CO_2 and High CO_2 scenarios to predict OA impacts in the future representing RCP 2.6 and RCP 8.5, respectively. RCP 2.6 characterizes the optimistic scenario in which immediate action is taken and annual global GHG emissions

peaks within a decade (year ~2025) but is then drastically reduced. While this pathway of strong mitigation of GHG emissions is unlikely given the current state of progress, it is the closest amongst the RCP scenarios to simulate conditions if we were to achieve targets set in the recent 'Paris Agreement' at the 2015 United Nations Framework Convention on Climate Change Conference of the Parties (COP 21). RCP 8.5 characterizes the current emissions trajectory where nations continue to develop their economy and the industrial sector using fossil fuels as the primary source of energy. This pathway is often referred to as the "business as usual" scenario, where no shift is made to reduce carbon emissions and invest in sustainable and renewable energy sources. Since this study focuses on the exploring the sensitivity of multi-climatic stressors impacts, fishing is assumed to be at level required to achieve maximum sustainable yield for each species in all the scenarios.

We acknowledge that OA can have effects on other biochemical (e.g. ATP production) and physiological processes (e.g. acid-base regulation) which can have downstream effects not directly linked to life history traits (e.g. bioenergetics) (Le Quesne and Pinnegar, 2012; Waldbusser et al., 2016). However, we constructed our model to link OA effects to physiological processes that can then be directly tied to life history traits that affect population dynamics. While OA effects on organism biology are generally complex, our model uses more generalized models in order to make comparisons about uncertainties.

2.3. Modelled species

We chose 10 commercially exploited invertebrate fisheries species distributed in either the Northwest Atlantic or the Northeast Pacific (Table 2) (initial species distributions can be found in Supplementary Fig. S2). Some species were distributed across both regions. This allowed us to compare results both across and within ocean basins. Invertebrate species were chosen as current knowledge suggests they are more sensitive to changes in pH than finfish (Kroeker et al., 2013). We chose 5 mollusc species and 5 crustacean species, spanning various taxonomic groups including: crabs, lobsters, prawns, oysters, mussels, clams, and cephalopods. Bottom environmental data was used for all demersal species, while surface environmental data was used for the only pelagic species included in our analysis—*D. pealeii*.

First, we present our results for the impacts of OA on species abundance from a multi-stressor model by including results from models run with and without OA impacts. In other words, we isolate the impacts of OA from other climate change stressors (i.e. temperature and oxygen) by taking the difference in abundance between model results with OA and without OA (hereon labelled OA and No OA scenarios,

Table 2

Species analyzed for the impacts of OA.

| Common name	Species name	Ocean basin distribution	Taxon group for OA impacts
American cupped oyster	*Crassostrea virginica*	Atlantic	Molluscs
American lobster	*Homarus americanus*	Atlantic	Crustaceans
American sea scallop	*Placopecten magellanicus*	Atlantic	Molluscs
Blue mussel	*Mytilus edulis*	Atlantic	Molluscs
Dungeness crab	*Metacarcinus magister*	Pacific	Crustaceans
Longfin inshore squid	*Doryteuthis pealeii*	Atlantic	Molluscs
Northern prawn	*Pandalus borealis*	Arctic, Atlantic, Pacific	Crustaceans
Pacific geoduck	*Panopea generosa*	Pacific	Molluscs
Snow crab	*Chionectes opilio*	Atlantic, Pacific	Crustaceans
Coonstripe shrimp	*Pandalopsis dispar*	Pacific	Crustaceans
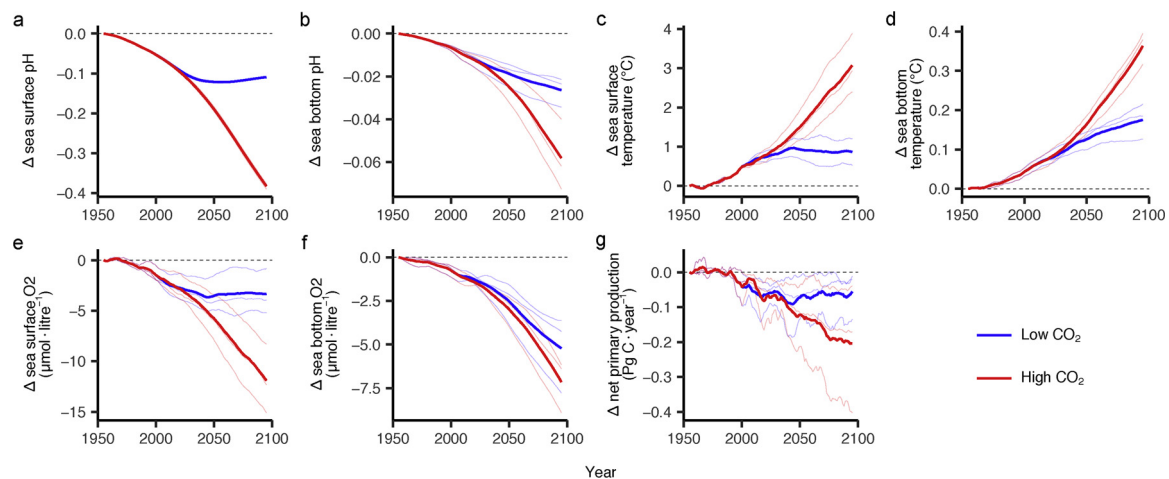
Fig. 2. Projected changes in ocean variables used as the main biophysical drivers in our model. Thin lines are projections from each of the three earth system models used (GFDL, IPSL, MPI) while thick lines are multi-model means. Projections are smoothed using 10-year running means.

respectively) impacts for each year (Fig. 1b). We then present full model results to put those OA effects into context of the overall effects of expected global environmental change.

3. Results

3.1. Projected changes in climate stressors

Global earth system models project changes to both sea surface and bottom environmental conditions and at a greater rate under high CO_2 emissions. Globally, average sea surface pH is projected to decrease by as much as 0.4 units, an increase in acidity of 140% relative to 1950 (Fig. 2a). Average change in sea bottom pH is projected to change by only as much as 0.06 units, yet still presents an increase of 14% in acidity (Fig. 2e). The magnitude of acidification will vary across ocean basins. The three other main drivers (temperature, oxygen, and primary production) of species biomass production in our model are projected to drastically change in high CO_2 scenarios (Fig. 2). For example, sea surface temperature is projected to increase by up to 4 °C by 2100, while bottom temperature is projected to increase by up to 0.4 °C. Change in net primary production was most variable across models and projections show increases and decreases across different ocean basins (Fig. 2d and Supplementary Fig. S3). In low CO_2 scenarios, the rate of change for many of these biophysical drivers is projected to decline and level off by 2050.

3.2. Responses to ocean acidification and global change

We used American lobster (*H. americanus*) to demonstrate how changes in temperature and ocean acidity affect life history parameters. Increases in either temperature or ocean acidity decreases the maximum body size and increases the von Bertalanffy growth parameter K (Fig. 3a and b). Compounded effects of temperature and acidity further reduce maximum body size (e.g. Sheridan and Bickford, 2011), but show diminishing rates of change as it approaches the asymptotic initial body size at time 0. Temperature and acidity combine to then increase the growth parameter K as von Bertalanffy's theory predicts that the rate of approaching the maximum body size of smaller individuals (and individuals with a smaller maximum body size) is faster (thus higher K) (von Bertalanffy, 1957). Additionally, temperature and acidity increase the growth rate with the trade-off of a reduction in body size (Atkinson, 1994; Sheridan and Bickford, 2011). Temperature effects on mass-specific growth rate (dB/dt from Eq. (1)) show that smaller individuals initially grow much faster (Fig. 3c) while larger individuals will grow much slower with increased temperature (Fig. 3d and e). The rate of

increased growth due to temperature effects on smaller individuals diminishes with greater change in stressors (temperature and acidity), while there is a negative synergistic effect on growth rate from multiple stressors for larger individuals.

Impacts of OA on both growth and survival were projected to reduce species' abundance under the high CO_2 scenario by the end of the 21st century (Fig. 4). Specifically, the combined effects of OA on growth and survival are projected to generally decrease species' abundance by as much as 10% (American cupped oyster) by year 2091–2100 relative to 1996–2005, while under the low CO_2 scenario there are negligible (change of < 1%) effects on abundance for most species. Pacific geo-duck abundance showed the most sensitivity to OA under the low CO_2 scenario, decreasing by ~ 4% (Fig. 4h). Interestingly, Dungeness crab abundance initially decreased due to OA but effects diminished by the end of the simulation (Fig. 4e). This pattern is likely due to a greater net increase of suitable habitat relative to the loss of habitat, leading to a spatial expansion of range size.

Changes in abundance over time when only OA impacts on growth were included closely follows the abundance for the combined effect of OA on growth and survival (Fig. 4). When impacts to both survival and growth were considered, changes in abundance were amplified. The magnitudes of OA impacts on abundance were variable but most species show a negative response to OA. Our results suggest that species abundance is more sensitive to the effects of OA on growth (mechanistic model) than the effects of OA on survival (correlative model).

Trends of changes in abundance with the different structural OA relationship models (Fig. 1a) were consistent across species, and differences between the relationship models were more pronounced under the high CO_2 scenario (Fig. 5; Supplementary Fig. S4). For most species (with the exception of Pacific geoduck), changes in abundance were small (< 1%) under the low CO_2 scenario across all relationship curves (Fig. 5a; Supplementary Fig. S4). In the example using American lobster in the high CO_2 scenario, abundance decreased by < 1% with the linear relationship, while the exponential relationship showed slow declines in abundance initially, but reached a 'tipping point' beyond which abundance declined more rapidly to > 2% (Fig. 5b). Changes in abundance under the 'adaptation' scenario were generally small and did not elicit a significant response.

Overall impacts to abundance due to all climate change stressors included in our model (e.g. OA, temperature, oxygen, primary production) showed high variability across species, with decreases greater than 40% (e.g. longfin inshore squid) and increases reaching 100% (e.g. northern prawn) by 2100 (Fig. 6). Only four of the ten species showed decreased abundance while the other six species showed increased abundance in the high CO_2 scenario. Half of the species showed greater
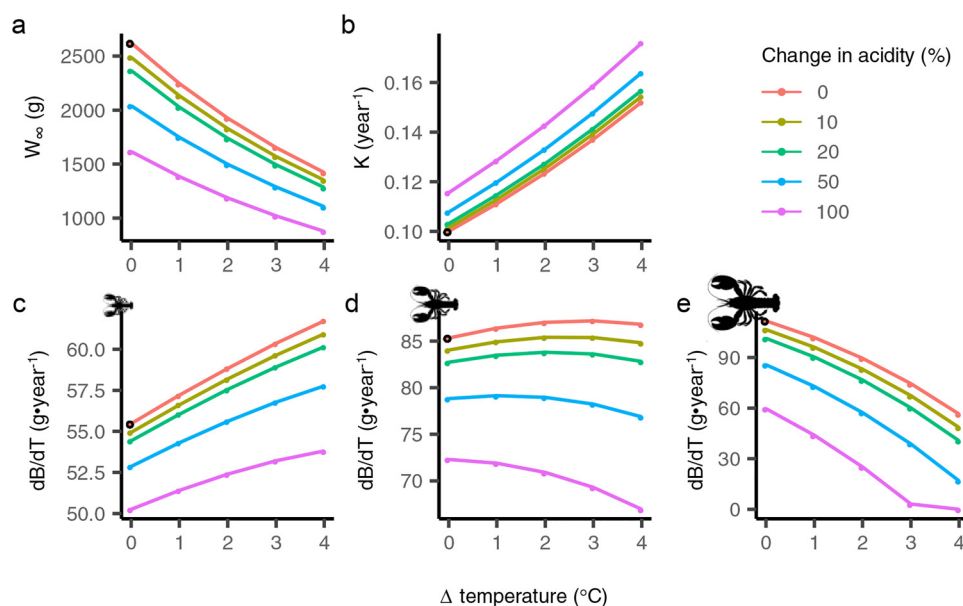
Fig. 3. Effects of changes in temperature and ocean acidity on life history parameters in American lobster (*H. americanus*): a) maximum body weight, b) von Bertlanffy growth parameter K, and growth rate for c) small (100 g), d) medium (250 g), and e) large individuals (1000 g). Black circles represent initial conditions with no change in temperature or acidity.

than 5% change in abundance in the low CO_2 scenario, suggesting that these species may be sensitive to even small changes in environmental conditions. OA showed consistently negative impacts on abundance across most species with greater differences between OA and no OA models in the high CO_2 scenario. Mollusc species were more sensitive to OA than crustacean species, with the exception of blue mussels and coonstripe shrimp.

We used American lobster once again as an example to show the biogeographic changes under the high CO_2 scenario. The distribution of American lobster shows negative impacts to its southern range (Fig. 7a). Areas in the Gulf of St. Lawrence and areas farther offshore show increased abundance. However, the net effect of the changes in the geographic distribution is an overall decrease in abundance (Fig. 6b). OA effects appear to be greatest in more northern and periphery areas of their geographic range (Fig. 7b). However, areas with greater OA effects correspond with areas of increased abundance, suggesting that OA may be limiting population growth and range expansion in response to other climate change drivers (i.e. temperature).

3.3. Sensitivity to uncertainty

Results from the DBEM showed varying levels of sensitivity to each source of uncertainty for each species. We quantified the range of projected changes in abundance for each source of uncertainty and found that changes in abundance were most sensitive to the uncertainty in the structural relationship between [H$^+$] and life history traits (i.e. linear, exponential, adaptation) (Table 3). We expected scenario uncertainty (RCP 2.6 and 8.5) to be greatest as it essentially indicates diverging pathways for global CO_2 concentrations, and this had the second highest average range of uncertainty (Table 3).

With other sources of structural uncertainty, our results were moderately sensitive to the choice of modeling approach, i.e. mechanistic effects on growth versus correlative effects on survival. Our results were relatively robust to the various earth system models. Sensitivity to parameter uncertainty was the smallest, suggesting our results are relatively robust to the magnitude of OA effects. This is an important finding as we used parameters for OA effects that were derived from meta-analyses for broad taxonomic groups. However, American cupped oyster showed very high uncertainty when different OA effect sizes were used.

The sensitivity to each level of model uncertainty was highly variable across species. Coonstripe shrimp showed the greatest range of uncertainty for all categories except parameter uncertainty (Table 3) where they were affected by OA equally with the different effect sizes used (Table 1). This was surprising as they also showed a significantly large negative response to OA (Fig. 4). While results from other species suggest that our model is robust to OA parameter uncertainty, it is not true for all species. American cupped oyster abundance was most sensitive to parameter uncertainty with a range of 13.1% between outputs, but overall trends were consistently negative (Table 3). Furthermore, our results suggest that species most vulnerable to OA may be the ones that show greater negative effects of OA but are less sensitive to parameter perturbations, such as Pacific geoduck and coonstripe shrimp.

4. Discussion

Our results present an analysis of the assumptions and uncertainties in modelling the biophysical impacts of OA using a spatially explicit model. Results of changes in abundance show sensitivity to all levels of uncertainty tested, although this varied with species and the type of uncertainty. In modelling OA effects, our results were sensitive to important assumptions of impacts on different life history rates, structural relationship between [H$^+$] and life history rates, and parameter estimates. OA impacts on abundance were consistent across species and generally showed a negative relationship with increased acidity (Fig. 4). Any measured increase in abundance due to OA was associated with the low CO_2 scenario and generally small (Table 3). However, some species increased in overall abundance in response to all global change stressors (Fig. 6). This trend is a result of the ability of a species to disperse and recolonize habitats that become more favourable with environmental change.

Temperature-driven geographical shifts and range expansion could overshadow any small negative effects of OA. Temperature effects can outweigh effects of OA on performance such as on growth and calcification (e.g. McNeil et al., 2004; Paul et al., 2015). Organism responses to temperature and OA interactions are complex across species, and previous studies have revealed synergistic, additive, and antagonistic interaction effects (Harvey et al., 2013; Kroeker et al., 2014; Munday et al., 2009). However, there have yet to be any empirical studies that show that temperature-driven geographical range shifts can outweigh any negative impacts of OA. Our results show overall increases in abundance for some species due to temperature-driven range shifts despite the negative effects of OA (Fig. 6). OA effects on Dungeness crab abundance appear to diminish with greater increases in abundance
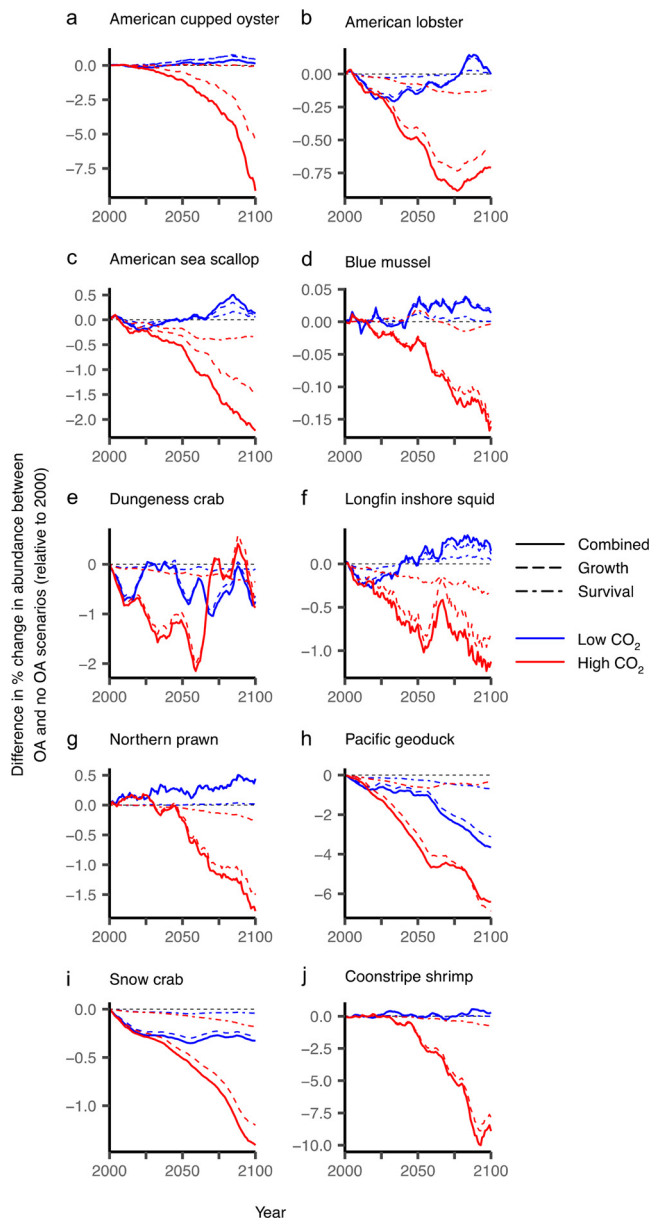
Fig. 4. Projected changes in species abundance (relative to 2000) due to OA impacts on growth, survival, and both combined for two climate change scenarios using GFDL earth system model. Abundances are smoothed by 10-year running means.

Fig. 5. Projected changes in American lobster (*H. americanus*) abundance (relative to 2000) due to OA under different assumptions for the relationship between OA and changes in both life history parameters (growth and survival) for two climate change scenarios, low CO_2 (a) and high CO_2 (b), using GFDL earth system model. Abundances are presented as 10 year running averages.

after year ~2065, suggesting that range expansion outweighs the effects of OA (Figs. 4e and 6e). Furthermore, such increases in abundance are not ubiquitous across the species range and may only apply to certain areas (e.g. poleward limits of geographical range), whereas other areas may see significant decreases (e.g. equatorward limits of geographical range) (Fig. 7).

Variability in our model results shows the importance of parameter selection, uncertainty, and the various underlying assumptions when integrating OA effects in species distribution models. Previous studies that have incorporated OA usually address uncertainty by using a range of effect sizes, typically derived from meta-analyses and empirical studies (Ainsworth et al., 2011; Cheung et al., 2011). Our results suggest that our model is generally robust to OA parameter uncertainty, but some species were highly sensitive to parameter perturbations.

Using generalized parameters across taxonomic groups is sufficient for broad-scale analyses or comparisons (e.g. Lam et al., 2014), but integrating species-specific data into models is essential when
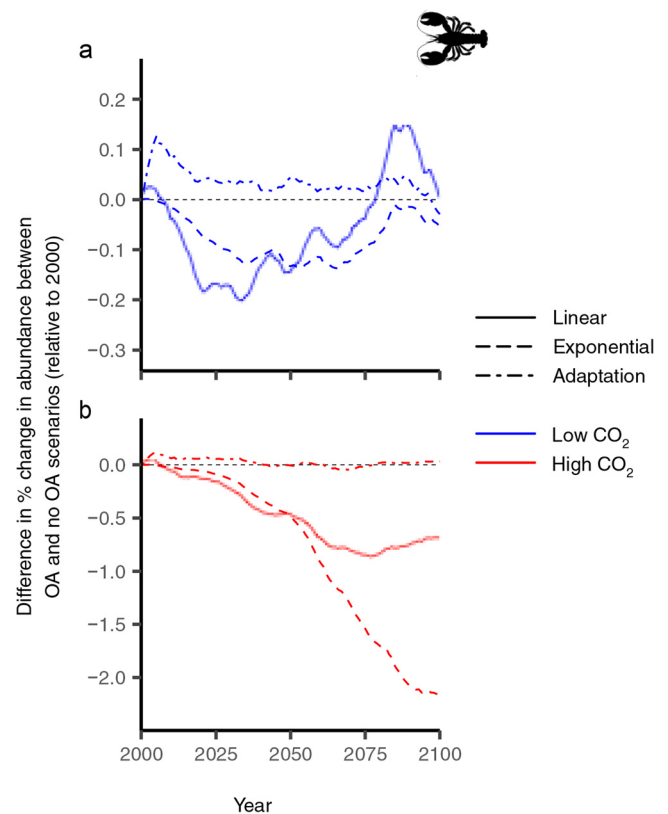
evaluating individual species for management purposes—especially for species that are highly sensitive to sources of uncertainty. With the growing literature on impacts of OA on marine life, projection models can utilize updated empirical data as input parameters to provide more accurate representations of OA effects (Ries et al., 2009).

Incorporating OA effects on different life history traits and the downstream effects on abundance provides novel insight to the alternative approaches that must be considered when constructing models (Kroeker et al., 2017). A mechanistic approach requires an understanding of the drivers and underlying biophysical processes and is therefore more difficult to incorporate, as more information is typically required. However, with a greater understanding of the mechanisms at play and the specific information needed, the responses to OA may be more realistic and accurate. Alternatively, correlative models offer a more straightforward approach, and are often easier to interpret. Correlative models may provide equally accurate results without the additional assumptions needed to incorporate mechanistic processes. Our model results indicate that the mechanistic approach has greater effects on abundance, even when the parameters used for survival were much greater (i.e. molluscs; Table 1). The correlative approach provides a more direct effect of OA on population dynamics, but assumes that underlying OA effects on physiological processes translate to changes in survival.

Using a mechanistic approach relates OA to changes in aerobic scope and the subsequent trade-offs with other life history parameters (e.g. growth rate, maximum body size, survival) (Pörtner, 2008). For example, natural mortality was modelled to be dependent on growth traits and temperature (Eq. (9)). Indirect effects of OA on other traits—such as fecundity—also emerge as we model them as a function of body size. The mechanistic approach allows us to address some of the
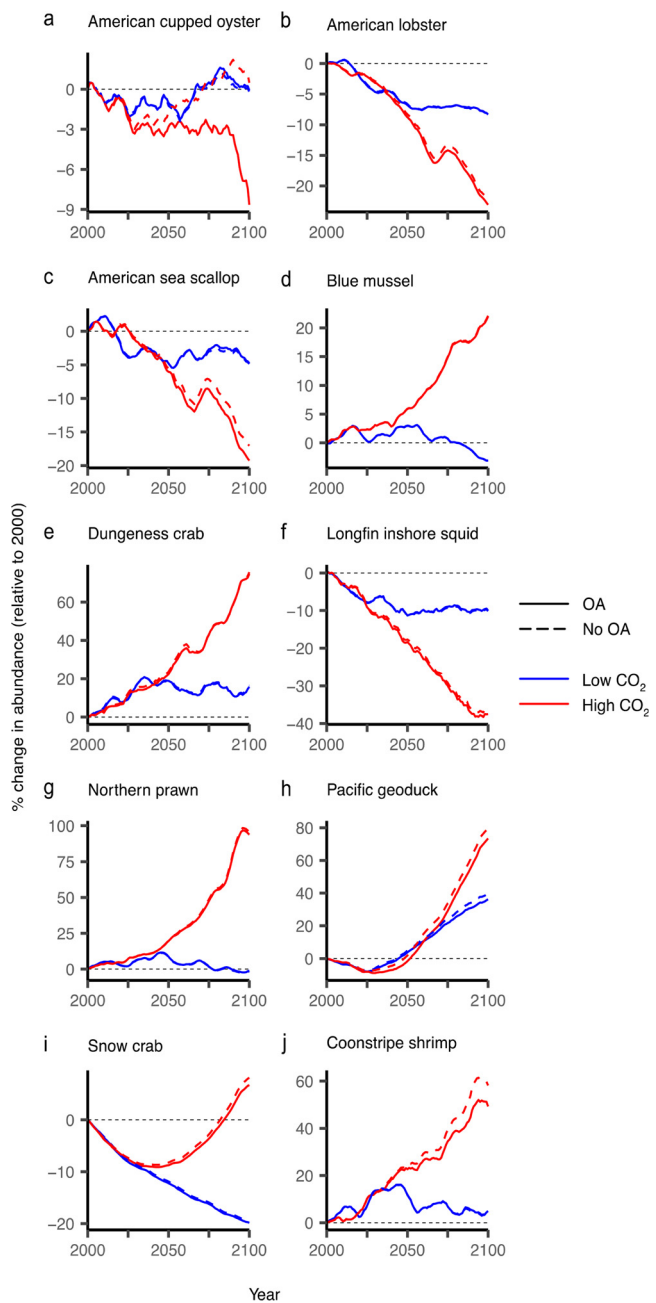
Fig. 6. Projected changes in abundance (relative to 2000) for model simulations with OA (solid lines) and without OA (dashed lines) impacts on growth and survival under two climate change scenarios. Changes in abundance are presented as multi-model averages across the earth system model used (GFDL, IPSL, MPI) and smoothed using 10 year running averages.

responses to environmental change (e.g. Clark and Sandblom, 2013; Lefevre et al., 2017) these tend to be much more complex, requiring a deeper knowledge of the mechanistic processes. Indeed, future studies should test the sensitivity of the DBEM to various equations of natural mortality and physiological processes with more experimental evidence. Using both correlative and mechanistic models allows our model to address generalized OA effects on population dynamics, while incorporating effects on organism biology that can have profound effects at the population level.

Few studies have considered the relationship between changes in OA and organism responses when modelling OA impacts on biological systems. The rule of parsimony favours a linear relationship, yet there is evidence of varying relationship curves (e.g. Anthony et al., 2011; Kleypas et al., 2006; Ries et al., 2009). This is especially important with greater changes in OA. For example, using the exponential relationship as a 'threshold' or 'tipping point' scenario, responses are much greater with high acidification but the onset of responses only occurs with a certain degree of acidification (Fig. 5). Tipping points for OA impacts can have drastic consequences to marine ecosystems and can manifest in ways such as direct impacts on physiological processes (Monaco and Helmuth, 2011) to indirect impacts on habitat availability (Sunday et al., 2017). Furthermore, experimental studies often focus on acute changes in pH, yet natural OA is a combination of gradual declines in the average pH and dynamic, more extreme temporal fluctuations in pH. Gradual changes in pH may favour species with high evolutionary potential (Lohbeck et al., 2012; Sunday et al., 2011) and more extreme fluctuations in pH may favour species with wide pH range tolerance (Ellis et al., 2016; Haigh et al., 2015). With knowledge of the evolutionary potential and OA tolerance of a species, future studies could apply a combination of an 'adaptation' model and alternative relationship curves to better represent long-term effects of OA on species distribution and abundance.

Species distribution models are valuable tools for projections of future global change, for both natural environments and the societies that depend on ecosystem goods and services. In addition to being some of the most susceptible organisms to OA, we evaluate marine invertebrates as they are ecologically important as key intermediate links to ecosystem structure and function (Fagerli et al., 2013; Reed, 2002; Steneck et al., 2002), and important economic resources as some of the most valuable fisheries species (Cooley and Doney, 2009; FAO, 2016). Biophysical projection models can then be coupled with socioeconomic scenarios that present possible management regimes for fisheries resources (e.g. Costello et al., 2016). Our model does not incorporate feedbacks of fisheries responses (e.g. profitability, management, activity) to changes in stock biomass, but it is an essential component to accurately model the dynamic interplay between environmental and anthropogenic pressures and responses of fisheries stocks and ecosystems. Results from projection models can also help inform future decisions and link to policies and agreements—e.g. projections of climate change impacts on global marine fisheries have shown the importance of meeting international targets to reduce emissions for both fisheries catch (Cheung et al., 2016b) and revenues (Lam et al., 2016). There are a number of studies that provide projections of the potential OA impacts to marine fisheries through extensive literature reviews and risk analyses frameworks (Branch et al., 2013; Ekstrom et al., 2015; Le Quesne and Pinnegar, 2012; Mathis et al., 2015). We envision the use of our results to develop a better understanding and potentially reducing the uncertainty with projecting OA impacts on living marine resources.

Our results of scaling OA effects from physiology to population biogeography provide useful insight to the underlying uncertainties and sensitivities. Constructing projection models such as the one here requires sound theoretical and empirical information. Further progress in reducing uncertainties can be made with more integration across disciplines and communication between the inputs and outputs needed by experimental biologists, ecologists, and modellers. For example, data from ocean acidification and warming experiments were used in a

complexities of OA effects and how it scales from physiology to population biogeography. However, OA affects many other physiological processes and life histories and are highly variable across species; current knowledge of the exact mechanisms and trade-offs between life histories are still not fully understood and there are other competing models (Kroeker et al., 2013; Pörtner et al., 2006; Ries et al., 2009). Pauly's (1980) model for natural mortality was chosen over other alternative empirical equations (e.g. Gislason et al., 2010; Then et al., 2015) because of its simplicity and the availability of life history parameters for the invertebrate species considered here. Physiological models used here were chosen because they provide a parsimonious representation, despite not being ubiquitous across all species. While there are other working hypotheses for modelling physiological
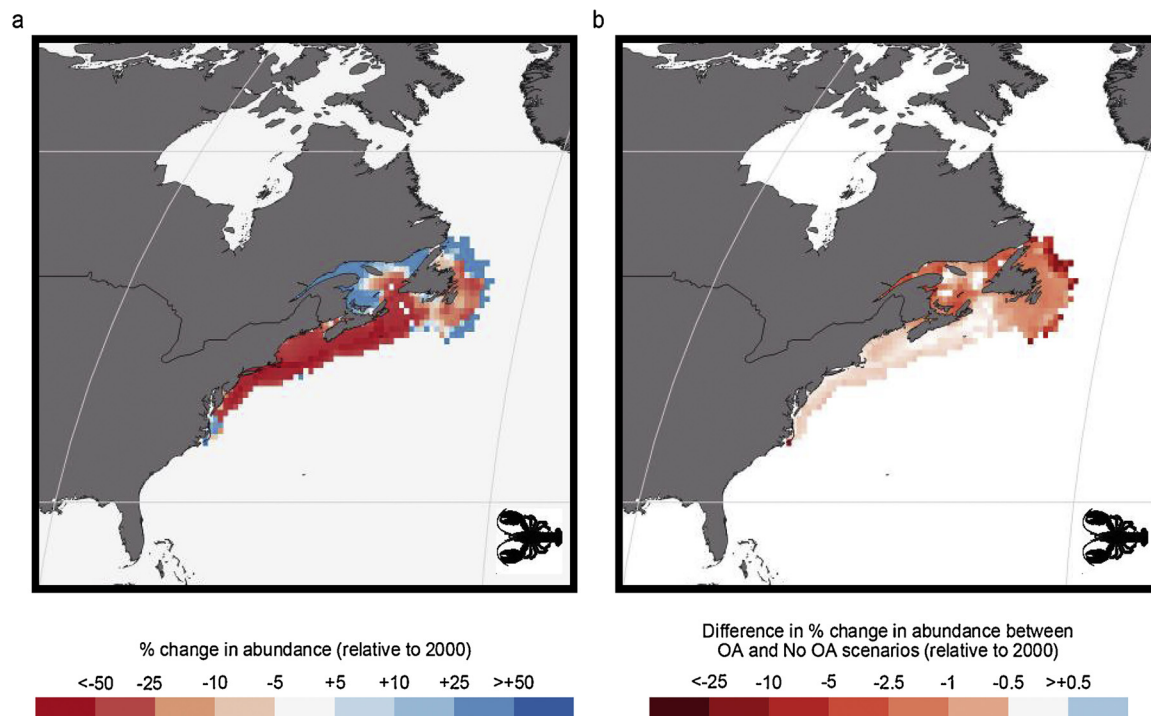
Fig. 7. Biogeographic changes in American lobster (*H. americanus*) abundance by year 2100 in response to a) changes in all climate stressors (i.e. pH, temperature, O_2, primary production), and b) isolated impacts of ocean acidification (OA).

projection model to estimate potential impacts to species distribution and abundance, all in one synthesized paper (Queirós et al., 2015). With accelerated OA and climate change leading to the emergence of more downstream consequences, it is essential to continue to reduce uncertainties of projection models to help inform mitigation and adaptation strategies.

Table 3

Magnitude of the output range of percent changes (with minimum and maximum values in parentheses) in abundance due to ocean acidification (OA) with each source of uncertainty tested in our model.[a]

	Structural			Parameter	Scenario	
	i. Mechanistic vs. correlative	ii. OA relationship form	iii. Earth system models	iv. OA effect size	v. RCP 2.6 vs. 8.5	*Mean range of species uncertainty*
American cupped oyster	4.6	6.1	1.9	13.1	8.1	**6.8**
	(-4.7, -0.1)	(-14, -7.9)	(-9.8, -7.9)	(-21, -7.9)	(-7.9, 0.2)	
American lobster	0.5	1.4	0.3	0.5	0.7	**0.7**
	(-0.6, -0.1)	(-2.1, -0.7)	(-0.7, -0.4)	(-1.2, -0.7)	(-0.7, 0.0)	
American sea scallop	1.0	4.0	1.5	2.7	2.3	**2.3**
	(-1.3, -0.3)	(-6.1, -2.1)	(-2.1, -0.6)	(-4.8, -2.1)	(-2.1, 0.2)	
Blue mussel	0.1	0.2	0.0	0.1	0.1	**0.1**
	(-0.1, 0.0)	(-0.3, -0.1)	(-0.1, -0.1)	(-0.2, -0.1)	(-0.1, 0.0)	
Dungeness crab	0.2	6.7	2.2	0.5	0.2	**2.0**
	(-0.3, -0.1)	(-7.0, -0.3)	(-2.5, -0.3)	(-0.8, -0.3)	(-0.5, -0.3)	
Longfin inshore squid	0.6	1.7	0.5	0.5	1.3	**0.9**
	(-0.9, -0.3)	(-2.8, -1.1)	(-1.1, -0.6)	(-1.6, -1.1)	(-1.1, 0.2)	
Northern prawn	1.1	4.0	0.8	1.9	2.0	**2.0**
	(-1.3, -0.2)	(-5.6, -1.6)	(-1.6, -0.8)	(-3.5, -1.6)	(-1.6, 0.4)	
Pacific geoduck	6.2	3.5	5.8	0.2	2.7	**3.7**
	(-6.6, -0.4)	(-9.7, -6.2)	(-6.2, -0.4)	(-6.4, -6.2)	(-6.2, -3.5)	
Snow crab	1.0	0.8	0.3	1.5	1.1	**0.9**
	(-1.2, -0.2)	(-2.2, -1.4)	(-1.4, -1.1)	(-2.9, -1.4)	(-1.4, -0.3)	
Coonstripe shrimp	7.6	9.9	9.5	0.1	9.7	**7.4**
	(-8.3, -0.7)	(-19.2, -9.3)	(-9.3, 0.2)	(-9.3, -9.2)	(-9.3, 0.4)	
Mean range of model uncertainty	**2.3**	**3.8**	**2.3**	**2.1**	**2.8**	

[a] Values shown are percent changes for the annual 2091–2100 average relative to 2000. The default scenarios/parameters held constant when testing each source of uncertainty were: i) including both mechanistic and correlative OA impacts; ii) baseline linear relationship between OA and effect size (Fig. 1a); iii) NOAA's GFDL earth system model; iv) mean effect size for OA impacts on growth and survival (Table 1); and v) high CO_2 scenario (RCP 8.5).

writing the report, or the decision to submit the article for publication.

Acknowledgements

The authors acknowledge funding support from MEOPAR through the COARNET project as well as *OceanCanada*, a partnership supported by the Social Sciences and Humanity Research Council of Canada. W.W.L.C. also acknowledges funding support from the Nippon Foundation-UBC Nereus Program and the Natural Sciences and Engineering Research Council of Canada. We thank Rashid Sumaila for his insights in this study.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.07.007.

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